

On the Origin and Migration of the Stinging-Cells in Craspedote Medusæ.

By

Charles L. Boulenger, M.A.(Camb.),
Lecturer on Zoology in the University of Birmingham.

With Plates 42 and 43 and 5 Text-figures.

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1. INTRODUCTION.

Lewis Murbach (1), in 1894, definitely established the fact that the stinging-cells of the Hydromedusæ have the power of active movement in the tissues by the formation of pseudopodial processes from the cnidoblasts.

These observations were confirmed by K. C. Schneider¹ (2) who published a detailed account of the development of nematocysts in *Agalmopsis* and other Siphonophora, and in his paper stated emphatically that:

“Alle Nesselzellen der Siphonophoren entstehen an locali-

¹ Schneider, as early as 1890, pointed out the fact that developing nematocysts were excessively rare in the tentacles of *Hydra*, and suggested that they might be formed on the body of the animal. He did not, however, pursue the subject any further (*vide* “Bibliography,” 3.)

sierten Bildungsherden, von denen aus sie in einem bestimmten Entwicklungsstadium als Wanderzellen auf die Verbrauchsstätten überwandern."

The subject has been recently revived by Jovan Hadži (4) in a remarkable paper in which he records his observations on the thread-cells of marine hydroids. Hadži's results are of the greatest interest, as he was able to examine the living tissues as well as preserved material. His main conclusions are as follows :

(1) The thread-cells of hydroids are not formed "in situ" but in the ectoderm of the cœnosarcal branches, where, on account of the thick perisarcal investment, they can obviously not become functional.

(2) When completely developed, except for accessory structures such as the cnidocils and the stalks, they migrate to the important nematocyst batteries on the tentacles. This migration can take place in two different manners. In simple forms, e.g. *Campanularia*, the thread-cells move actively by means of their pseudopodia, making their way between the ectodermal cells of the colony. In *Tubularia* however, they adopt a quite different method of locomotion : from the ectoderm of the cœnosarc they force a way through structureless lamella and endoderm into the cavity of the hollow stem, whence they are carried by the current caused by the flagella of the endoderm cells to the hydranths. Here the thread-cells re-enter the tissues and migrate actively by their own movements to the ectoderm of the tentacles.

In a recent paper, whilst describing the structure of the Egyptian lacustrine medusa, *Mœrisia lyonsi* (5), I called attention to the fact that large nematocysts were to be found in abundance among the endoderm cells of the manubrium. Being at a loss to account for their presence in this position I cut sections of a large number of specimens, careful examination of which convinced me that I was dealing with a case similar to that investigated by Hadži in Hydroids. As this phenomenon has not been described previously in

Medusæ, I have endeavoured in this paper to give as complete an account as possible of the origin and distribution of the nematocysts of this form.

The material used for this investigation was collected by Dr. Cunningham and myself in Lake Qurun, and was carefully fixed either with osmic acid or with hot corrosive sublimate. Sections were cut by the ordinary paraffin method and a number of stains were tried, the best results being obtained with hæmatoxylin followed by eosin; this produced an excellent double-stained effect, the eosin bringing out the nematocysts and rendering them most conspicuous. Borax carmine followed by picro-indigo-carmine was another good differential stain and iron-hæmatoxylin was useful when examining sections of the developing Medusæ. The work in connection with this paper was carried out partly in the Morphological Laboratory at Cambridge and partly in the Zoological Laboratory of Birmingham University. I wish to express here my sincere thanks to Professor F. W. Gamble, who very kindly read through my manuscript and made many valuable suggestions.

2. THE STINGING-CELLS OF THE ADULT MEDUSA OF MÆRISIA.

As mentioned above, a striking feature of the anatomy of this medusa is the presence of numerous thread-cells¹ in the endoderm at the base of the manubrium. At first it seemed possible to account for their occurrence in this unusual position by assuming that these stinging-capsules were used ones taken in by the jelly-fish together with its food. On careful consideration this view was found to be quite untenable, for—

¹ The nomenclature of the different parts of the stinging-cells is somewhat cumbersome and complicated; moreover, the various names have been used very loosely. In this paper I have employed the terms thread-cell or stinging-cell for the whole structure comprising the nematocyst (the actual stinging capsule), and nematoblast (the cell in which the former is embedded, and of which the cnidocil and the stalk are parts).

(a) The nematocysts found in the endoderm are always undischarged.

(b) Favourable sections show them to be accompanied by their nematoblasts.

(c) The nematocysts are never to be found near the free margins of the endoderm cells, but, for the most part, between the more basal portions of these cells near the structureless lamella.

These thread-cells can, obviously, not become functional in this position, and the only possible explanation of their occurrence here is that they are making their way from their place of origin to some battery where they can be of use.

At this point it may be well to review the distribution of stinging-cells in the ectoderm of the manubrium. The chief battery is situated around the mouth-opening; here the thickened ectoderm forms a circular lip crowded with nematocysts, and constitutes a powerful organ of offence (Pl. 42, figs. 3 and 4). The ectoderm of the remainder of the manubrium proper consists of a single layer of low, closely fitting epithelial cells with occasional isolated nematocysts; it is to be noticed that here, as well as on the oral lip, interstitial cells are completely absent. At the base of the manubrium is the broad stomach, the ectoderm of which is considerably thickened and forms the conspicuous gonad.

Interstitial cells and developing thread-cells being absent from the more distal parts of the manubrium, the question arises—Where are the nematocysts of the oral battery formed, and how did they attain their position in this region? An answer is, I think, afforded by the study of the distribution and arrangement of the nematocysts in the manubrial endoderm. The greatest number of these are to be found just below the region of the gonad, where, in most specimens, numerous thread-cells are to be met with among the large digestive cells of the endoderm. In this position one can usually find a number of dark-staining interstitial cells, some of which contain rudiments of stinging-capsules, and are obviously nematoblasts (Pl. 42, figs. 1 and 2).

In the more distal parts of the manubrium we find nematocysts to occur less abundantly, and their position in the endoderm is very regular, the longer axes of the capsules being parallel with the structureless lamella and their broader ends directed towards the mouth of the medusa (Pl. 42, fig. 3). Previous authors have shown this orientation to be characteristic of migrating thread-cells, and we must come to a similar conclusion; namely, that they are making their way from the base of the manubrium to the oral battery. This view is confirmed by an examination of the tissues of the mouth region, where one can often find thread-cells actually forcing their way through the structureless lamella to the oral battery. Here they take up their definitive position and develop accessory structures, e. g. cnidocil and stalk, from the nematoblast. A stinging-cell occasionally turns aside before reaching the oral region (Pl. 42, fig. 4), and passing through the lamella, forms one of the isolated nematocysts to be met with in the more proximal parts of the manubrial ectoderm.

The route followed by the thread-cells of the medusa is readily explained. These structures, when the nematocysts are completely developed, are of considerable size, whereas the ectoderm of the manubrium is very low, and, moreover, forms a very definite epithelium of closely fitting cells, between which the large stinging-cells could scarcely force a passage. We need, therefore, not be surprised that they adopt the much easier way between the large and loosely packed cells of the endoderm.

From the above account it appears, therefore, that in *Mœrisia* the nematocysts of the oral battery of the medusa are developed in the endoderm at the base of the manubrium; this does not necessarily imply that the nematoblasts are themselves endodermal in origin, as will be explained in the section of this paper which deals with the development of the medusa-bud.

In addition to that surrounding the mouth opening, the main nematocyst batteries of the medusa are situated on the

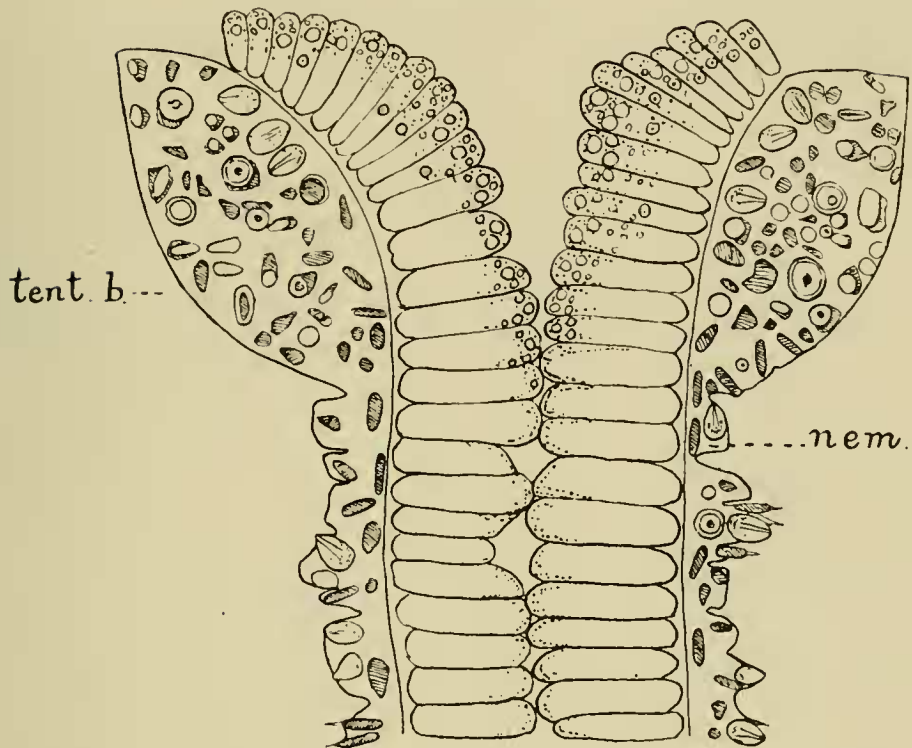
four perradial tentacles suspended from the umbrella edge. These tentacles are slender and of great length when fully extended; at their bases they are swollen to form the very conspicuous ocellar bulbs, each of which bears on its ex-umbrellar surface a bright red eye-spot. The tentacles are hollow, their cavities being continuous with that of the circular canal; the ectoderm is thickened at regular intervals to form conspicuous transverse rings crowded with nematocysts, and becoming very noticeable and almost bead-shaped when the tentacles are fully extended.

On examination of sections and maceration preparations of these organs, one is again struck by the almost complete absence of nematoblasts or other interstitial cells, and we are driven to the only possible conclusion, namely, that the stinging-cells have developed elsewhere and have migrated to the batteries on the tentacles. The large, eye-bearing bulbs at the bases of the tentacles immediately suggest themselves as possible nematocyst "factories," and sections of these structures show that such a function must be assigned to them (Text-fig. 1).

An ocellar bulb consists of a mass of thickened ectoderm crowded with small, irregularly shaped cells and nematocysts in various stages of development. The fully formed thread-cells are devoid of enidocils or other accessory structures, and the capsules are never orientated so as to lie at right angles to the surface; we must, therefore, conclude that they do not become functional in this region. In the centre of the bulb the nematocysts lie in all directions, but near the base of the tentacle we find a distinct tendency for these organs to be arranged with their longer axes parallel with the structureless lamella, a position, as mentioned above, characteristic of migrating thread-cells.

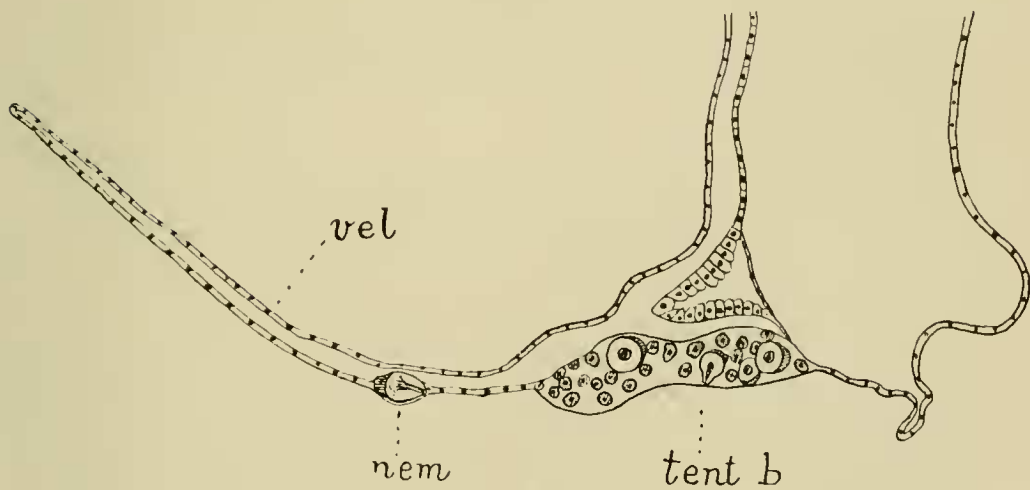
The above-mentioned facts lead us to the conclusion that the stinging-cells of the tentacles, like those of the oral battery, are not developed "in situ," but migrate into these organs from "factories" situated in a more central position on the medusa, in this case from the ocellar bulbs, whence a

TEXT-FIG. 1.



A longitudinal section through the ocellar bulb and the base of a tentacle of *Mærisia lyonsi*. *tent.b.* Ocellar bulb. *nem.* Nematocyst migrating into the tentacle.

TEXT-FIG. 2.



Section of the umbrella edge of *Mærisia lyonsi* showing the velum (*vel*) and part of an ocellar bulb (*tent.b.*) *nem.* Nematocyst migrating towards the edge of the velum.

continual stream of thread-cells are being poured forth. The majority of these are obviously on the way to their tentacular batteries, although occasionally one may wander into the velum, as shown in Text-fig. 2.

3. MIGRATING STINGING-CELLS IN OTHER MEDUSÆ.

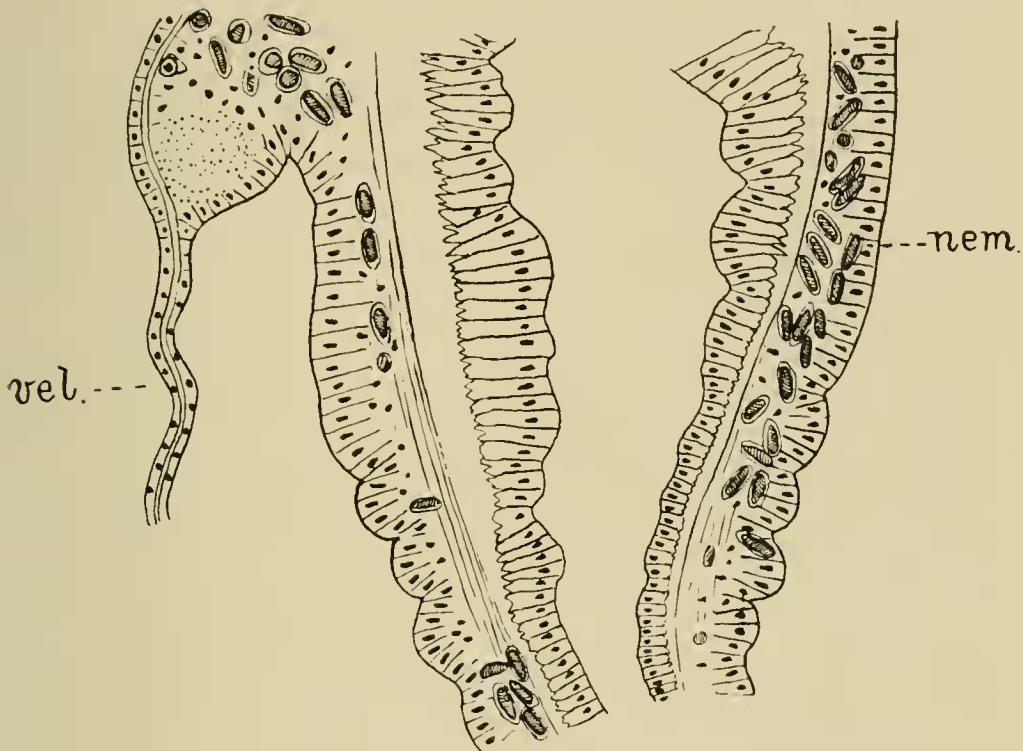
In the preceding paragraph I have attempted to prove that the conspicuous bulbous swellings which occur so constantly as the bases of the tentacles of craspedote Medusæ have an important function besides that of bearing the ocellar sense-organs. In such craspedote Medusæ as are devoid of tentacle-bulbs, e. g. the Trachomedusæ and Narcomedusæ, we find that the edge of the umbrella is provided with a special thickened ring of ectoderm, containing stinging-cells, sometimes known as the "nettle-ring." Further, those forms in which the tentacles take their origin some distance from the margin of the bell on the exumbrellar surface are provided with special bands of nematocysts, called peronia, which connect the above-mentioned nettle-ring with the bases of the tentacles. These facts make it very tempting to assume that the marginal ring of nematoblasts replaces the ocellar bulbs in function, and reference to the figures of this organ, given by various authors, seems to show that this assumption is probable correct. It is a point which requires special investigation, and I will at present merely refer to the evidence which is at my disposal.

The Hertwigs' most accurate figure of the umbrella edge of *Carmarina* (6, Pl. iv, fig. 5)¹ shows the nettle-ring to be packed with thread-cells without definite orientation; at the base of the tentacle, however, a number of nematocysts are drawn arranged in such a manner that there can be little doubt that they are migrating from the marginal ring to the batteries on the tentacle. I have examined sections through the tentacles of a medusa of the same genus, and

¹ I should like to express my indebtedness to Dr. S. F. Harmer, F.R.S., for calling my attention to this figure.

these showed the same orientation of nematocysts as in the specimen figured by the Hertwigs. I have figured one of these sections (Text-fig. 3) chosen from a series in the Cambridge Morphological Laboratory; comparison with that of *Mœrisia* (Text-fig. 1) is very instructive.

TEXT-FIG. 3.



A longitudinal section through the base of a tentacle of *Car-marina* sp. *vel.* Velum. *nem.* Nematocyst migrating through the ectoderm of the tentacle.

Günther's figure of *Limnocnida* (7, fig. 6) shows that a similar migration of thread-cells must occur in that medusa.

4. THE DEVELOPMENT OF THE MEDUSA OF *Mœrisia*.

As shown above, the nematocysts of the main stinging batteries of *Mœrisia* are formed in two quite distinct positions in the medusa: (a) The manubrial endoderm, (b) the ectoderm of the ocellar bulbs.

In order to properly understand the origin of these

different situations of the stinging-cell factories it is necessary to examine the development of the medusa in some detail.

Until recently the accepted view of the development of the gonophores of the Hydromedusæ was based essentially on L. Agassiz's observations on *Syncoryne mirabilis*, published in 1862 (8). His account of the process was confirmed by Hertwig (9), Weismann (10), and almost all later workers on the same subject, and is essentially that to be found in the majority of modern text-books. The following description of the development of the medusa of *Bougainvillea* is taken from one of the latter (18), and represents the prevailing ideas on the subject :

The medusa-bud makes its first appearance as a simple hollow bud formed by the evagination of the two layers of the mother-polyp. Multiplication of the ectodermal cells at the apex results in the production of a lens-shaped mass of small cells which sinks below the level of the superficial ectoderm, pressing the endodermal wall in front of it into the shape of a cup. This mass of ectoderm is called the entocodon (Glockenkern), and a cavity which appears in its interior is the rudiment of the subumbrella cavity. It is followed by an invagination of the superficial ectoderm, the wall between the new cavity thus formed and the subumbrella cavity being the future velum. Growth of this subumbrella cavity results in an approximation of the endodermal walls of the coelenteron, and these ultimately fuse into an endoderm lamella except where the circular and radial canals are to lie. The upgrowth of the manubrium from the floor of the subumbrella cavity, the formation of the tentacles and the perforation of the velum and manubrium complete the formation of the medusa.

A. Goette (11) has recently made a thorough examination of the development of the gonophores of *Podocoryne carnea* and a large number of other hydroids, and has published a long and elaborate paper on the subject. As the result of his investigations this author concludes that the current views on the origin of these structures are quite

erroneous, and states that carefully cut series of sections of developing medusa-buds show that a double-walled cup of endoderm is not present at any stage; moreover, the four radial canals arise from four unconnected pouches of endoderm which grow out separately, although simultaneously, from the cœlenteron of the bud, and are completely independent of the entocodon. The endoderm lamella is formed later by the lateral extensions of the solid edges of these pouches, which finally fuse with one another. Again, an invagination of the superficial ectoderm does not take place and the forecast of the velum is present at a quite early stage, and is then represented by the flattened apex of the bud, where the superficial ectoderm and the distal wall of the entocodon come into contact with one another.

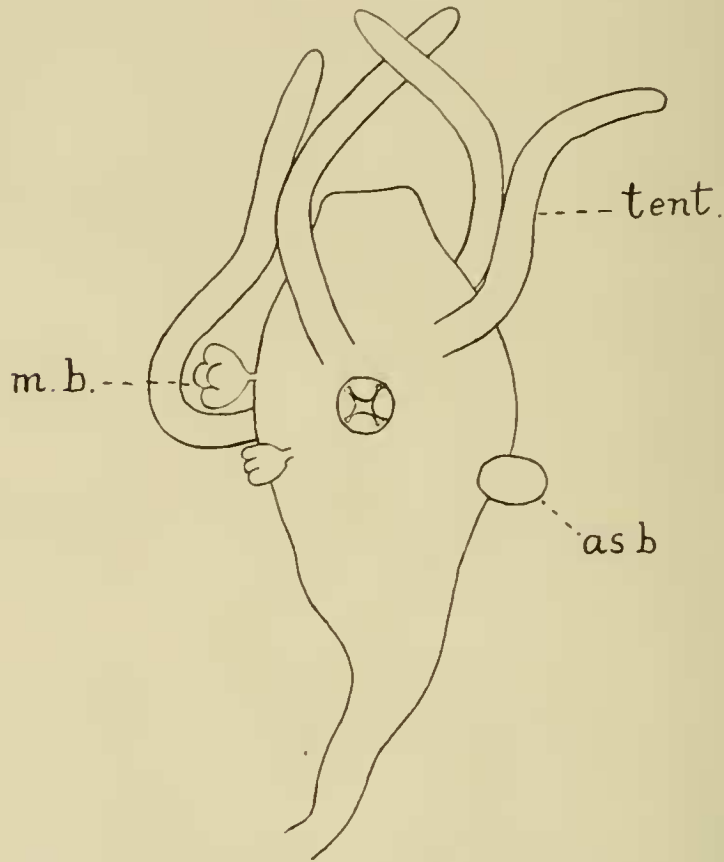
Goette's paper has not received (at any rate in this country) the attention which so important a communication deserved, and the only confirmation of his results is that of his pupil, Walter Richter (13), who, acting on his professor's advice, worked out the development of the gonophores in Rhizophora, Physalia, and other Siphonophora and described a similar origin for these structures in this division of the Hydromedusæ.

In my account of the anatomy of the hydroid stage of *Mœrisia* I did not go into this subject with any detail, but merely stated that the development of the medusa-buds seemed quite typical, the growth of the cavity in the entocodon causing the approximation of the endodermal walls of the bud.

The examination of a large series of sections during my investigation of the origin of the nematocysts has shown me that this statement was erroneous, and that the development of the medusa of this form agrees very closely with that of *Podocoryne carnea* as described by Goette. My error, like that of other writers on the same subject before Goette, was due to the use of optical sections, and partly to the examination of single sections of the buds instead of complete series.

In *Mærisia lyonsi* the medusa-buds are to be found scattered irregularly on the broadest region of the hydranth between the bases of the tentacles (Text-fig. 4), thus differing in position from the asexual lateral buds, which are restricted in the majority of cases to the more proximal parts of the body.

TEXT-FIG. 4.



Outline sketch of a hydranth of *Mærisia lyonsi* to show developing gonophores and a small asexual bud. $\times 30$. *tent.* Tentacle. *m.b.* Gonophore with conspicuous ocellar bulbs. *as.b.* Asexual lateral bud.

The ectoderm of this region is somewhat deeper than in other parts of the hydroid, the boundaries of the large musculo-epithelial cells are difficult to detect, and the whole tissue is crowded with interstitial cells, for the most part nematoblasts, containing nematocysts in various stages of development. The endoderm consists of large vacuolated

digestive cells, between which are numerous characteristic gland-cells with coarse granular contents which stain deeply.

The first indication of a developing medusa-bud is to be traced in the ectoderm, an accumulation of interstitial cells causing this layer to project slightly outwards. The endoderm soon begins to take part in this bulging out of the tissues, and owes its increase in area chiefly to the proliferation of the large cells, but partly also to the accumulation of interstitial cells, which are to be found in the endodermal tissue in the region of a developing bud. These cells I believe to be ectodermal in origin, for favourable sections show occasional interstitial cells to migrate from the ectoderm through the structureless lamella into the endoderm. In this way a hollow, double-layered bud is formed (Pl. 43, fig. 5) by a process which cannot be called one of simple evagination, but in some respects resembles that of the formation of the early stages of the lateral buds in *Hydra*, as recently described by J. Hadži (14).

As long ago as 1891, W. B. Hardy (15) showed that in the early development of the gonophores of *Myriothela phrygia* there was a certain mixing up of endodermal and ectodermal cells to form a kind of blastema, and it seems probable that further investigations will prove that the production of a bud from the body of a hydroid is by no means so simple a process as has been made out by some authors.

The entocodon is next formed by the proliferation of the ectoderm at the apex of the bud, and consists of a small-celled plug of tissue between ectoderm and endoderm. Four pouches of endoderm are arising simultaneously from the cœlenteron; from them the radial canals of the adult are to be derived. Reference to fig. 6 will show that there is nothing of the nature of a double-walled endodermal cup in the bud, one side of the obliquely cut section showing a radial pouch, the other the contact of the entocodon with the superficial ectoderm.

It is to be noticed that this superficial ectoderm has not

changed in character and is identical in structure with that covering the hydranth, consisting of large epithelial cells, interstitial cells, and nematoblasts, with occasional nematocysts.

The independent origin of the four radial pouches of endoderm is still more obvious in figs. 7, 8, and 9, which are three sections in different planes of a slightly later stage. In the transverse section (fig. 7) the entocodon is seen to be roughly square in section, being in contact with the superficial ectoderm at the four corners (interradii); the four perradial pouches are thus completely separated from one another. A median longitudinal section (fig. 8) through the perradii at this stage shows, of course, two of the endodermal pouches separated by the hollow entocodon. As pointed out by Goette, it is from the examination of such a section, independently of others of the series, that the idea arose that a double-walled cup of endoderm was formed by the growth of the entocodon. A tangential section taken a short way on either side of this median section will naturally show a single pouch only, as illustrated in fig. 9. In this stage the forecast of the manubrium is already conspicuous, and is, of course, clothed externally by the proximal wall of the entocodon.

The four endodermic pouches continue their growth outwards to the very tip of the bud, and at their terminations push out the ectoderm, causing the formation of four perradial bulbous projections, which are the forecasts of the ocellar bulbs. A section, therefore, taken through a perradius gives rise to the false idea of an invagination of ectoderm towards the entocodon (Pl. 43, fig. 10). The four bulbs are very conspicuous features of the external anatomy of the medusa, even at this relatively early stage of development (Text-fig. 4).

The formation of the endoderm lamella is exactly as described by Goette for *Podocoryne carnea*; the central part of each endodermal pouch becomes a radial canal, the large cells at the edges growing out to form two solid wings of endoderm, which meet similar projections from the other

pouches at the interradii (Pl. 43, fig. 7, *r.p.e.*¹). The ring-canal is formed by the fusion of the distal ends of the radial pouches at the bases of the bulbous swellings referred to above.

Up to this point the histology of the two layers has been quite constant; the superficial ectoderm has retained its original character and remains crowded with interstitial cells of all kinds, in striking contrast with the small-celled regularly arranged tissues derived from the entocodon. The endoderm lining both the cœlenteron and the radial pouches consists of large clear cells, with somewhat indefinite outlines and containing numerous large nutritive spheres, which stain deeply with iron-hæmatoxylin; a few irregularly shaped interstitial cells are to be found, most numerous between the endoderm cells lining the manubrium.

In the last stage of the development described above we found all the organs of the adult medusa already well defined, with the exception of the tentacles. From this point onwards the more important changes are to be found in the structure of the umbrella, which now grows rapidly, especially in the region between the ocellar bulbs and the base of the manubrium, so that the superficial ectoderm loses its characteristic features, as noticed above, and gives rise to a low, small-celled epithelium covering the external surface of the bell. The endoderm behaves in a somewhat similar fashion. The ocellar bulbs, however, remain unaltered; the endoderm still consists of large irregular cells with nutritive spheres; the ectoderm is still crowded with interstitial cells, thread-cells, and nematoblasts, the latter increasing rapidly and forming new nematocysts, both large and small (Text-fig. 5).

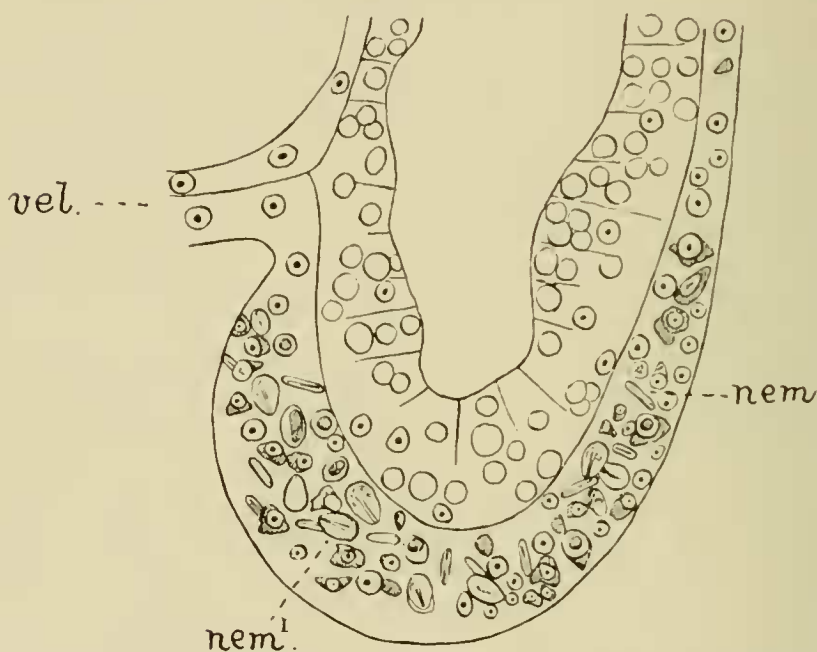
The ocellar bulbs give rise to the tentacles, their main function being obviously that, already mentioned on p. 768, of supplying these organs with stinging-cells.

In the preceding paragraphs I have tried to emphasise the fact that beyond an increase in the actual number of cells, the ectoderm of this region has remained practically unchanged throughout the development of the gonophore. The

tentacular nematocysts of the fully-formed medusa thus arise in the interstitial cells derived from the ectoderm of the parent hydroid.

The ocellar bulbs are, of course, retained throughout the life of the medusa, and, as mentioned above, keep on supplying the tentacles with stinging-cells; they are no doubt especially active during the regeneration of these organs. This explains the constant presence of such swellings at the

TEXT-FIG. 5.



A longitudinal section of an ocellar bulb of *Mærisia lyonsi* just before the development of a tentacle. *vel.* Velum. *nem.* Small nematocyst. *nem.¹* Large nematocyst.

bases of the tentacles of the Hydromedusæ, as well as their early appearance and relatively enormous size in the developing medusa-buds. The function of bearing the ocellar sense-organs must be a secondary one, for such bulbs are conspicuous in the formation of medusæ which do not possess ocelli, e. g. *Podocoryne carnea*, concerning which Goette (11, p. 19) remarks:

“Bald nach der Fertigstellung des Velum verdickt sich das Ectoderm jedes Randwulstes dicht über dem Velum zu

einem vorspringenden Polster, das den Ocellarbildungen anderer Medusen entspricht, aber, wie schon die älteren Beobachter (Allman, 16; Grobben 17) feststellten, keine Ocellen entwickelt."

In a young medusa of *Mœrisia* a short time before its liberation the manubrium is still without a mouth opening, and is clothed externally by a single layer of low ectodermal cells (Pl. 43, fig. 11), the internal lining consisting of large clear endoderm cells containing nutritive spheres and occasional irregularly shaped interstitial cells. The latter become more numerous as development proceeds, and some can be clearly recognised by their enlarged nuclei to be sex-cells. These at a later stage, no doubt, become transferred to the ectoderm of the stomach region, and by their further division form the gonad. Owing to the absence of individuals of the right age, I am unable to state how the transference of sex-cells from one layer to another takes place. I have never met with them migrating through the structureless lamella, and it is quite possible that the transference is a passive one, similar to that described by Goette in the male gonophores of *Hydractinia* (11, p. 70). In the youngest free-swimming medusæ examined by me the endoderm of the slightly swollen stomach had lost its small cells, and was separated by a very thin lamella from the ectoderm, which contained a few rows of developing sex-cells.

The endoderm slightly distal to this region had retained a number of interstitial cells, some of which prove to be obvious nematoblasts and contained developing nematocysts. These are, of course, the rudiments of the fully formed stinging-cells, which, as described in the first part of this paper, are to be found in the endoderm, just below the stomach of the adult medusa, and which later migrate to the battery at the oral extremity of the manubrium.

From this we must infer that the nematoblasts of the manubrium arise in the endoderm of the developing gonophore in exactly the same way as do the sex-cells; like the latter they are able to migrate through the tissues of the medusa.

When we remember the similar origin of the two kinds of cells from undifferentiated interstitial cells, we need not be surprised that they both possess the same powers of active movement.

That the thread-cells are identical in origin with the sex-cells is further emphasised by the fact that in exceptional cases part of the testis of *Mœrisia* can give rise to a nematocyst battery instead of producing sperm-cells, as shown in Pl. 43, fig. 12.

Both kinds of cells are first to be recognised in the endoderm of the medusa-bud; this does not necessarily imply that they originate in that layer; in my account of the early development of the gonophore, I showed that interstitial cells of the ectoderm occasionally migrate through the structureless lamella of the hydranth and become incorporated among the proliferating cells of the endoderm. It is probable that these cells or their derivatives give rise to the sex-cells and nematoblasts.

In my description of the anatomy of *Mœrisia lyonsi* (5), I mentioned that exactly the same types of nematocysts were to be found in the medusa as in the hydroid; in this paper I hope to have proved that they are not only identical in structure, but actually originate from the same cells. This fact is one which might be of use in systematic work on the Hydromedusæ, where the assignment of Medusæ to hydroids is often only a matter of inference; a careful comparison of the nematocysts of the two stages should be of great value in this connection.

5. GENERAL CONCLUSIONS.

(1) The stinging-cells of the medusa of *Mœrisia lyonsi* are not developed "in situ" on the principal batteries, but migrate to their final positions on the oral lip, or on the tentacles.

(2) The stinging-cells of the oral battery are formed in the endoderm of the manubrium, just below the stomach; those

of the tentacles in the ectoderm of the conspicuous ocellar bulbs at the terminations of the radial canals.

(3) There is reason to believe that the bulbous swellings at the bases of the tentacles have this function throughout the craspedote Medusæ. In the sub-divisions *Trachomedusæ* and *Narcomedusæ*, they are probably replaced by the thickened ring of thread-cells on the margin of the bell.

(4) The development of the gonophores of *Mærisia* takes place in the manner described by Goette for other hydroids. There is no double-walled cup of endoderm at any stage, the radial canals and the endoderm lamella being derived from four separate pouches of endoderm, which grow out simultaneously from the cœlenteron of the simple bud.

(5) The stinging-cells of this medusa are developed from cells, which, like the sex-cells, arise directly or indirectly from the ectoderm of the parent hydranth.

BIRMINGHAM,

June 19th, 1910.

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This bibliography includes only those works actually mentioned in the text of my paper; for a more complete list of literature I must refer the reader to the memoirs of Hadži (4) and Goette (11).

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EXPLANATION OF PLATES 42 AND 43,

Illustrating Mr. C. L. Boulenger’s memoir “On the Origin and Migration of the Stinging-cells in Craspedote Medusæ.”

PLATE 42.

EXPLANATION OF LETTERING.

ect. Ectoderm of the manubrium. *end.* Endoderm of the manubrium.
gl.c. Gland-cell. *nem.* Endodermal nematocyst. *nem.¹* Nematocyst of the oral battery. *nem.²* and *nem.³* Migrating nematocysts. *s.l.* Structureless lamella. *test.* Testis.

Fig. 1.—A longitudinal section of the proximal part of the manubrium of the medusa, *Mærisia lyonsi*, to show the nematocysts in the endoderm.

Fig. 2.—A transverse section through the same region.

Fig. 3.—A longitudinal section of the distal part of the manubrium showing the oral battery and a stinging-cell (*nem.*³) migrating through the endoderm towards it.

Fig. 4.—A similar section showing a stinging-cell (*nem.*³) making its way through the structureless lamella to the ectoderm.

PLATE 43.

EXPLANATION OF LETTERING.

c.b. Cavity of the medusa-bud. *c.e.* Cavity of the entocodon, i. e. subumbrella cavity. *c.m.* Cavity of manubrium. *ect.* Superficial ectoderm of the developing gonophore. *end.* Endoderm of the same. *ent.* Ectoderm of the entocodon. *g.c.* Gland-cell. *i.c.e.* Interstitial cell of the endoderm. *nem.* Small nematocyst. *nem.*¹ Large nematocyst. *n.s.* Nutritive sphere of the endoderm. *r.p.e.* Radial pouch of endoderm. *r.p.e.*¹ Lateral solid extension of the same, which later forms the endoderm lamella. *s.c.* Sex-cell. *tent.b.* Tentacle-bulb. *test.* Testis. *v.* Velum.

Fig. 5.—Longitudinal section of an early stage in the formation of the gonophore of *Mærisia lyonsi* (cf. text, p. 775).

Fig. 6.—Tangential longitudinal section of a young bud showing the entocodon and a single radial endoderm pouch.

Fig. 7.—Transverse section of an older gonophore to illustrate the complete independence of the four radial pouches. The entocodon already has a large cavity (subumbrella cavity), and at *r.p.e.*¹ can be seen the solid extension of the edge of a pouch which later forms the endoderm lamella.

Fig. 8.—Radial longitudinal section through a similar (slightly younger) bud, showing two radial pouches of endoderm separated by the entocodon.

Fig. 9.—Tangential longitudinal section of the same medusa-bud; only a single pouch is shown.

Fig. 10.—Longitudinal section of an almost completely developed medusa to show the bulbous swellings at the termination of the radial pouches.

Fig. 11.—Manubrium of the same medusa under a higher magnification.

Fig. 12.—Section through the testis of an adult medusa, part of which has given rise to a stinging-cell battery.